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ORIGINAL PAPER

Intersexual food transfer among orangutans: do females test males for coercive tendency?

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Abstract Tolerated transfer of food among adults is rare among primates, except in humans. Here, we present data on a consistent pattern of tolerated intersexual transfer of food (held in hand, foot, or mouth by the owner) among adult orangutans, in two different natural populations (*Pongo abelii* and *Pongo pygmaeus wurmbii)*, based on ca. 9,000 h of focal observation per site. Although rare, intersexual food transfers were disproportionately from males to sexually active females and involved food that was equally available to both sexes. There was no evidence for direct trading of food for social favors (mating, grooming, or agonistic support) or for sharing under pressure of harassment. However, females frequently protested with loud screams when males, especially unflanged ones, attempted to take food they possessed, and also when males responded aggressively to their taking attempt. Since associations ended sooner when the female emitted noisy calls, a male who did not allow a female to take food from him risked losing the association. These findings support the hypothesis that by taking food, a sexually active female may test the male's tendency toward violence. Thus, intersexual food taking in orangutans is based on female leverage, resulting in a species-wide female entitlement to male "generosity". The inhibition of food defense required for this kind of transaction may also form the basis for sharing patterns among species in which nutritional benefits have become important, such as chimpanzees and perhaps human foragers.

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Introduction

In many birds and mammals, individuals transfer food to offspring or other members of the same reproductive unit (Clutton-Brock 1991; Brown et al. 2004; Feistner and McGrew 1989). In most of these cases, the donor receives an inclusive fitness benefit (Hamilton 1964). Sometimes, however, food is transferred toward individuals that are both independent and unrelated. This is especially common in humans (Wilson 1975; Hawkes 1993; Gurven 2004). The evolution of such peaceful food transfer ("food sharing"), where one individual relinquishes control over a food item in favor of another, is still little understood because by engaging in such seemingly altruistic acts, individuals incur costs that must somehow be recouped in order to be favored by natural selection (Wilson 1975; Stevens and Gilby 2004).

Among adult non-human primates, peaceful food transfer is rarely in the form of active provisioning by the original owner. Instead, primates "share" almost always in the form of unopposed taking ("tolerated theft"—Blurton Jones 1984, 1987; "relaxed claims"—de Waal 1989), in which the initiative is taken by the recipient. When a dominant takes food from a subordinate, the interaction is easily explained by the apparent imbalance of power. However, when an individual takes food from a larger, stronger, or more dominant conspecific, this can only happen without agonistic repercussion if the original owner inhibits its defensive response (Brown et al. 2004; de Kort et al. 2006). These interactions are the most puzzling.

Although food transfers among (non-related) adults from a dominant to a subordinate have been reported for other

primates in their natural habitat (e.g., bonobos—Kano 1980; Kuroda 1984; White 1994; Fruth and Hohmann 2002; capuchins—Perry and Rose 1994), they are both common and well studied in wild chimpanzees (e.g., Teleki 1973; Mitani and Watts 2001; Matsomoto-Oda 2002; Watts and Mitani 2002; Gilby 2006; Slocombe and Newton-Fisher 2005; Ohashi 2007; Hockings et al. 2007) and humans (e.g., Hawkes 1991; Smith and Bliege Bird 2000; Gurven 2004). To explain these interactions, three main hypotheses have been proposed. First, the sharing individual might be showing off his intrinsic viability by his food acquisition, and through this "costly signaling" gain in reputation (Hawkes 1991; Smith et al. 2003; cf. Kalishov et al. 2005; Scheid et al. 2008), with delayed returns in the form of increased access to mates or securing favors for themselves or their affinal and biological relatives. However, at present, there is no strong evidence in favor of this idea for non-human primates (but see de Waal 1989).

Second, sharing under pressure (Wrangham 1975) would give the food owner more time to feed on a highly nutritional food item than would be possible if it were defended. Indeed, Gilby (2006) found for Gombe chimpanzees that the sharing of meat, rare and highly valued food, reduced the cost of defending it from persistent beggars. However, this hypothesis cannot explain food transfer that does not follow distractive begging. Third, food transfer could be reciprocated or exchanged for another valued commodity such as grooming or agonistic support (most likely if the recipient is powerful). Indeed, in an experimental setting, de Waal (1989, 1997) found evidence for short-term reciprocation of food transfers in chimpanzees, as well as short-term exchange for grooming. Similarly, among male chimpanzees in the wild, food transfer was found to be more common between allies (Watts and Mitani 2002).

Food transfer between the sexes, in chimpanzees at least, is predominantly from male to female, and thus not reciprocal. Because males should easily be able to refuse begging by females, sharing under pressure is also hardly likely (unless the number of beggars is large). Moreover, there is, as yet, no evidence for exchange for either agonistic support or grooming by females. Instead, to explain such asymmetric interactions, Stanford et al. (1994) proposed another form of exchange, namely food in exchange for mating access. Although Kano (1980) and Kuroda (1984) had earlier reported this for bonobos, more detailed analyses in chimpanzees found no evidence for a direct trade (Mitani and Watts 2001; Matsumoto-Oda 2002; Gilby 2006). Thus, we still lack a well-tested universal explanation for intersexual food transfers among non-human primates.

Among orangutans, food transfer is common from mothers to dependent offspring (Jaeggi et al. 2008). However, here we report on the far less common intersexual food transfers among sexually mature individuals observed in two natural populations, one on Sumatra (Suaq Balimbing—*Pongo abelii*), and one on Borneo (Tuanan—*Pongo pygmaeus wurmbii*). In both populations, individuals of both sexes spend less than half of their time in association with other independent individuals, but associations are more common on Sumatra than Borneo (van Schaik 1999; van Noordwijk et al. 2009). In this system, several explanations can be excluded a priori. First, whereas two associating females might be closely related, this would be highly unlikely for a female–male dyad (van Schaik 2004; Goossens et al. 2006). Thus, by concentrating on intersexual food transfer, we can exclude nepotism. Second, exchange for agonistic support or grooming can be excluded because neither male nor female orangutans form coalitions or show other forms of cooperative behavior, and allogrooming is extremely rare (<0.05% of total time in association; unpublished data from both sites). Third, purely nutritional benefits, and thus also sharing under pressure, can be excluded. There is no consistent sex bias in possible food ownership because males and females show virtually no difference in their ability to collect the food items in the local diet, including those that are transferred (van Schaik et al. 2009 and unpublished data). As a result, the only possible explanations for intersexual food transfers in orangutans are food for sex and costly signaling, for neither of which there is currently much evidence among non-human primates, or an as yet undeveloped alternative. If the intersexual food transfers in orangutans can be understood, they may help to provide a more general explanation for food sharing in primates.

We defined food transfer as the transfer of (part of) a food item already collected by one individual to another individual, out of the first individual's hand, foot, or mouth, followed by continued eating by both participants in close proximity. This definition concurs with findings that primates distinguish between actual and potential ownership (cf. Kummer and Cords 1991; Jensen et al. 2007). Thus, we concentrate on those cases in which the original collector of the food item relinquishes control over (part of) it and allows another individual to take some. We exclude "co-feeding" situations where conspecifics take turns obtaining food from a large non-moveable food source not owned by either.

Methods

Data were collected in two long-term studies of orangutan behavior, at Suaq Balimbing (03°04′ N, 97°26′ E), on Sumatra, from February 1994 to September 1999 (van Schaik 1999; Singleton and van Schaik 2002) and at Tuanan

(2°09′ S, 114°26′ E), on Borneo (van Schaik et al. 2005), from July 2003 to May 2006. Focal animal follows were conducted, whenever possible from night nest to night nest, recording all social behaviors continuously and activities instantaneously at 2-min intervals (see also http://www.aim.uzh.ch/orangutannetwork.html). For both sites, only data by observers well-trained in recording social interactions were included in the analysis: in total 8,858 h of focal data at Suaq and 9,503 h at Tuanan. In Suaq, focal females and males were in mixed-sex party for 2,590 h, of which 1,428 h were spent feeding; in Tuanan, 1,782 and 998 h, respectively. Even though an attempt was made to record all social interactions, this is not always possible under field conditions and thus the data presented are a minimum estimate of the actual rate at which food is transferred from one individual to another. All statistical tests were based on frequencies; probabilities are two-tailed.

Results

At both sites, the majority of food-taking attempts among independent orangutans occurred between the sexes (Tuanan 84% of 43 attempts, Suaq 75% of 53); the other cases were between adult females, or between a non-offspring independent immature and an adult of either sex, but never between males. Actual intersexual food transfer was observed in 86% of 36 attempts in Tuanan and in 60% of 40 attempts in Suaq. All analyses below refer only to intersexual food transfer (attempts) among adults.

Of the actual transfers, 73% in Suaq and 97% in Tuanan took place when there were no other adult conspecifics in association, i.e., within 50 m. In Suaq, the frequency of transfers was proportional to the frequencies of mixed-sex associations with only a single male and a single female vs. those with additional adults (goodness-of-fit, $\chi^2;_1=0.021$, $P=0.885$), whereas in Tuanan, food transfer was even more likely in mixed-sex associations of only the two interacting adults than in those with additional adults (goodness-of-fit, $\chi^2;_1=8.73$, $P=0.003$). Thus, the majority of intersexual food transfer occurs in the absence of an audience and with only one adult (and perhaps one immature) as potential beggars.

At both sites, intersexual food transfer attempts were rather uncommon (Suaq 0.028 per hour spent feeding in intersexual association, Tuanan 0.036). In addition, at both sites, the majority of transfers involved food that was not of exceptional value with respect to its nutritional content or difficulty to obtain, and only some transferred items required some skill in finding and/or processing. In most cases, the transferred food was readily available at the location, including: (part of) a fruit (Tuanan 50%, Suaq 7.3% small fruit, 9.8% hard to process *Neesia*), vegetable matter such as vine stems (Tuanan 5.6%, Suaq 30.5%), or pieces of termite-infested wood (Tuanan 44.4%, Suaq 46%). (The only recorded case of meat transfer did not involve two adults, and the original owner was a female.) There is no indication in the data that any of the transferred foods were not also independently found, processed, and eaten by recipients at the same or other occasions. No strong sex difference in the likelihood of owning different kinds of food was detected in the focal observations at each site (see also van Schaik et al. 2009), and where there was some sex bias in the frequency of ownership of the transferred food, i.e., termite wood, females tended to own it more often than males. Yet, in both populations, females took food from a male without being opposed (tolerated food transfer) about twice as often as males from females (combined sites 29 vs.13, binomial test, $P=0.019$).

Recorded responses to a food-taking attempt between the sexes were (a) tolerated food transfer (55% of all 76 intersexual attempts in the sites combined), (b) protested food transfer (food is transferred, but owner shows protest by bites or slaps or other physical actions and/or loud vocalizations, 18%), (c) agonistic prevention (food is not transferred, 13%), or (d) quiet prevention in which the owner turned away (13%). In both populations, the same pattern of asymmetry was apparent, in that males and females differed in the relative frequencies of these responses to attempts by the other sex to take food (Fig. 1; Tuanan—Fisher's exact 4×2 test, $P=0.008$; Suaq $P=0.214$; combined $P=0.001$). When a male attempted to take food from a female, he was more likely to be met with an agonistic response (protested transfer + agonistic prevention vs. tolerated transfer + quiet prevention) than vice versa (Fig. 1; Tuanan—Fisher's exact 2×2 test, $P=0.007$; Suaq $P=0.155$; combined $P=0.003$). When a female attempted to take food from a male who reacted aggressively with an attempt to bite, the female responded with screaming

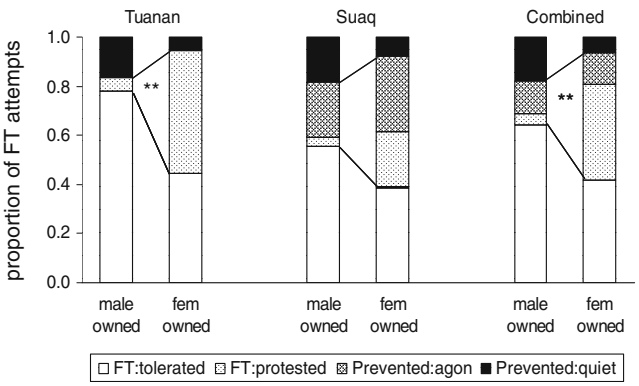

Fig. 1 Proportion of all intersexual food-taking attempts resulting in tolerated food transfer, protested food transfer, agonistic prevention, or quiet prevention for Tuanan ($N=18$ attempts from male-owned food and $N=18$ attempts from female-owned food), Suaq ($N=27$ male-owned and $N=13$ female-owned), and combined for both sites combined. Agonistic response = protested food transfer + agonistic prevention (see text)

(one observation in both populations), but when he just pushed her away (also counted as agonistic response), the female tended to move away. Moreover, males protested only physically and never gave loud vocalizations whereas females did both. Thus, females were less tolerant of male attempts to take food from them than males were toward females, resulting in more tolerated food transfers from a male to a female than from a female to a male in both populations.

In the two populations combined, 89% (68 of 76, Tuanan 100%; Suaq 80%) of intersexual food transfer attempts involved a sexually active female, i.e., a female who had no or a (nearly) weaned infant and mated "regularly". Indeed, sexually active females were significantly more likely than lactating mothers to be involved in an intersexual food transfer interaction than expected based on the number of hours they were observed in a mixed-sex party (Tuanan—goodness-of-fit test, $\chi^2;_1=8.8$, $P=0.003$; Suaq $\chi^2;_1=9.04$, $P=0.003$; sites combined $\chi^2;_1=19.47$, $P<0.001$). They were also more likely than lactating mothers to attempt to take food from a male in association (Tuanan—goodness-of-fit test $\chi^2;_1=3.83$, $P=0.05$; Suaq $\chi^2;_1=8.72$, $P=0.003$; sites combined $\chi^2;_1=12.68$, $P<0.001$). In Suaq, those lactating mothers who engaged in food transfer attempts were not successful, in contrast to sexually active females (zero in four attempts by lactating females vs. 16 in 23 attempts by sexually active females, Fisher's exact test, $P=0.019$). Thus, compared to lactating females, sexually active females were both more likely to engage in intersexual food transfers when in association with a male and more successful in taking food from males. In contrast, males in Suaq who attempted to take food from females did not do so more from sexually active females than from lactating mothers, but in proportion to association time (goodness-of-fit test, $\chi^2;_1=0.56$, $P=0.45$).

Despite clear indications that intersexual food transfers are almost entirely restricted to sexually active females, there was no evidence for increased mating frequency up to 3 h (the longest time frame that gave a reasonable sample size) after tolerated food taking by a female from a male. Compared with the mean copulation rate during mixed-sex parties (Tuanan—unflanged males 0.04 cop/h; flanged male 0.021 cop/h; Suaq—unflanged 0.077 cop/h and flanged 0.056 cop/h), there was no significant increase after a tolerated food transfer at either Tuanan, Suaq, or both sites combined (combined data, baseline vs. 3 h after food transfer—unflanged males $\chi^2;_1=2.26$, $P=0.133$, flanged males $\chi^2;_1=0.11$, $P=0.74$). Thus, we could find no evidence that males derive an immediate sexual benefit from allowing a female to take food from them.

However, being in association with a female is an obvious prerequisite for any mating by a male. Hence, it remains possible that a male's tolerance toward a female contributes to his future mating chances. Females have some means of terminating involuntary associations. First, 61% (11/18) of observed cases, when intervention by a flanged male ended an association, happened after the female had actively moved into the direction of a recent long call, which are emitted only by flanged males. Such "interventions" rarely involve active displacement since the mere arrival of the other male causes the first one to flee. After this, the female may remain in association with the newcomer, but more often goes her own way. Second, females may also increase the chance of an association-ending "encounter" through loud vocalizations drawing attention to their location. Indeed, at Tuanan, the site with the more complete data on this, female–male associations were far more likely to be terminated before the end of the day through an encounter with another male if there were loud vocalizations indicating its presence and location than if the association was quiet (Fig. 2; 31% of 58 vs. 12% of 66; Fisher's exact test, $P=0.014$). (Vocalization include screams, loud kiss squeaks, and grumps by the female and maybe her offspring, whereas males are mostly quiet during associations—except for rare calls directed at potential predators or observers, and even flanged males in consort strongly reduce their rate of long calling [Mitra Setia and van Schaik 2006].) Thus, loud protests of a female to a male trying to take food from her increased the male's risk that the association with her will end by a more dominant male's intervention.

Attempts by females to take food from unflanged males were roughly four times more common per hour in a mixed-sex association than attempts to take from flanged males (1/0.0284 h vs. 1/0.0074 h; Tuanan—goodness-of-fit test, $\chi^2;_1=2.08$, $P=0.149$; Suaq $\chi^2;_1=5.59$, $P=0.018$; combined $\chi^2;_1=8.30$, $P=0.004$).

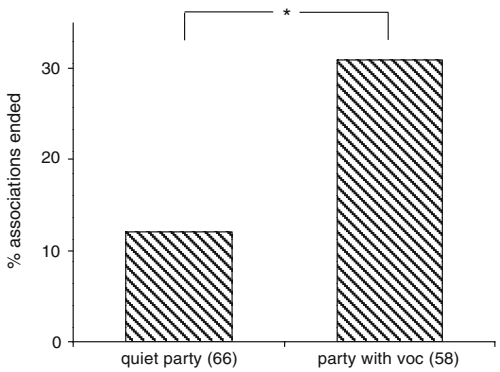

Fig. 2 Percentage of female–male associations that were terminated before the end of the day through intervention by another male when no loud vocalizations were given during the party (quiet parties) and when loud vocalizations were given, in Tuanan. Total number of mixed-sex parties given in *parentheses*

Discussion

The similar findings in the two orangutan populations indicate a consistent pattern, despite the low rates of food transfer among independent individuals. Moreover, observations on the Ketambe population of Sumatran orangutans corroborate the general pattern found for Tuanan and Suaq—a low frequency of asymmetric food transfer, mostly from males to sexually active females, involving food that is generally not special, and a more tolerant response by males to female taking attempts than vice versa (S.S. Utami Atmoko, personal communication).

As to the function of this intersexual food transfer, nepotism and exchange of food for agonistic support or grooming could be excluded a priori. The significant asymmetry also allowed us to exclude food-for-food reciprocity. We will now evaluate the costly signaling and food-for-sex hypotheses, and then develop a new interpretation.

Food transfer as costly signaling requires an active (honest) signal from the donor conveyed to an audience (Grafen 1990; Gintis et al. 2001). For the honest signal to reflect the phenotypic quality of the food owner, the food must be difficult (or risky) to acquire, as in chimpanzees (meat—e.g., Stanford et al. 1994; Mitani and Watts 2001; Watts and Mitani 2002; Gilby et al. 2006; raided crops—Hockings et al. 2007), and humans (e.g., Hawkes 1991; Bliege Bird et al. 2001; Smith et al. 2003). Because the signal's effectiveness should increase with party size, we expect costly signaling especially when the audience is large. Alternatively, the honest signal may convey the intent to establish or maintain a cooperative relationship (Gurven 2004). This "courtship feeding" would require that the donor actively donates food to others, as also seen in active food sharing among peers in some birds (von Bayern et al. 2007). In this second form, the value of the food is less important. Food transfer in orangutans cannot be considered costly signaling of either kind because the owner does not possess food items that are especially nutritious or difficult to acquire and there is usually no audience beyond the recipient, nor does the owner take the initiative to share.

We now turn to the food-for-sex hypothesis. Although most food sharing was with sexually active females, males did not gain immediate mating benefits. Instead, males may have benefited from maintaining the association longer by allowing females to take food, given that associations involving loud vocalizations were more likely to be terminated before the end of the day. Thus, although some exchange between tolerance and eventual mating opportunities cannot be excluded in orangutans, there was no evidence for a direct trading of food for sex. Unfortunately, the frequencies of observed matings and food transfers were too low to test whether a male's aggressiveness toward a female in the food-sharing context predicted his aggressiveness in the mating context.

Because none of the existing hypotheses did explain the patterns observed in this study, we will now develop an alternative explanation of the results by interpreting the main results. First, in both populations, females took food from males more often than vice versa, despite equal ownership, and females were far more likely to protest when a male took food from them than vice versa. This suggests that females may be gathering information about the male.

Second, the higher frequency (per hour in association) of food transfers from males to sexually active females as compared to lactating mothers, in both populations, is due to real variation in the females' initiative to interact with males. For instance, in Tuanan, lactating mothers never even attempted to take food from males, whereas in Suaq they rarely tried (relative to sexually active females) but were never successful. On the other hand, when males attempted to take food, they did not discriminate between mothers and sexually active females once in association. Because sexually active females initiated intersexual food transfers much more than nursing mothers, this suggests that these interactions over food serve to provide them with information about a male's disposition, relevant to assess the risks of violence in sexual interactions. The data suggest that the female estimates male coercive disposition by his responses in the food transfer context, which range from tolerating the taking of food through aggressively defending food to trying to take food from females.

Third, females exert some control over the association, by moving toward another male whose location is known through his long calls (Mitra Setia and van Schaik 2006; Delgado 2003) or by attracting him through loud vocalizations. The Tuanan data show that such loud vocalizations increased the chance that another male interfered in a female–male association and that females could increase the chance of interference by actively moving toward a flanged male's position. Thus, the females' loud protests of male attempts to take food from them may signal that they intend to end associations with intolerant or violent males.

Fourth, females are more likely to take food from unflanged than flanged males. Several lines of evidence suggest that females prefer the company of (dominant) flanged males over unflanged males. Unflanged males are more often reported to force matings with females (Fox 2002; Knott and Kahlenberg 2007), and sexually active females preferentially associate, engage in voluntary consortship, and initiate copulations with flanged males (Galdikas 1981; Schürmann 1982; van Schaik and van Hooff 1996), and actively approach their long calls (Mitra Setia and van Schaik 2006).

Taken together, these findings support the idea that the intersexual food transfer patterns in orangutans serve females' attempts to acquire information on a male's coercive tendency. Given that orangutan males, especially unflanged ones, often show violence in the sexual context, using his willingness to inhibit his tendency to defend food that he owns may serve as a test by the female of the male's inclination to be aggressive. The females' ability to exert some control over the prolongation of an association (and thus potential future mating opportunities for the male) provides them with the required leverage (Lewis 2002).

We, therefore, suggest that food transfers from males to females among great apes began as tests by females of male coercive tendencies, whereas the acquisition of highly nutritious food, such as meat in chimpanzees, is built on this original function. Nevertheless, orangutan females use this test too rarely to say that they do so systematically. Perhaps this is because they do not need to do so in the case of known males with whom they have an established relationship. This might also explain the higher frequency of attempting to take food from relatively young (and less well-known) unflanged males.

In the case of chimpanzees, where food transfers may be more common and involve highly nutritious food items, one may speculate that the original coercion avoidance function is also still present, along with the derived nutritional function. First, although ownership of the shared food, usually meat, is highly asymmetric, the absence of reports of sharing of nutritious plant foods, such as nuts, possessed more by females and shared widely with offspring (Boesch and Boesch-Achermann 2000), suggests that the asymmetry is intrinsic, as in orangutans. Second, most sharing was found from males to sexually attractive females in several populations (Mitani and Watts 2001; Matsomoto-Oda 2002; Ohashi 2007; Hockings et al. 2007). Even though this might represent investment into a future mating relationship as suggested by Tutin (1979), little evidence for a food-for-sex exchange exists to date. Third, females are often harassed by males (Muller et al. 2007; Wrangham and Peterson 1996), giving them an incentive to test males. Fourth, like female orangutans, female chimpanzees have the required leverage in that they have some control over their associations, at least in some populations (Goodall 1986; Hasegawa and Hiraiwa-Hasegawa 1990; Boesch and Boesch-Achermann 2000). Finally, there is some evidence that females associate more with males that are less violent and more affiliative and prefer mating with them (Tutin 1979; Matsumoto-Oda 1999; Boesch and Boesch-Achermann 2000; Stumpf and Boesch 2005). In sum, intersexual food transfers in chimpanzees may continue to function as tests of male character, in addition to their derived nutritional function. It is therefore possible that the testing of male intentions may be the original function of intersexual food transfer, to which later functions, including provisioning, were added.

Theoretical models of the cost and benefits of cooperation between individuals recognize, at least for humans, the threat of punishment or sanctions as a cost, which can be avoided by cooperation, in this case the inhibition of food defense (e.g., West et al. 2006; cf. Gurven 2004). Thus, the female orangutan's threat of a reduction in association time could be seen as a sanction against an intolerant response by the male. The clear indication that females have some control over their associations, despite sexual dimorphism and semi-solitary lifestyle, enables the enforcement of cooperation. This should lead to a general tendency of males to be “nice” to females, wherever females have leverage.

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